- 13. Miller, G. S. The families and genera of bats. Bull. US Natl Mus. 57, 1-282 (1907).
- Novacek, M. J. & Wyss, A. R. Higher-level relationships of the recent eutherian orders: morphologica evidence. *Cladistics* 2, 257–287 (1986).
- Beard, K. C. in Primates and their relatives in phylogenetic perspective (ed. MacPhee, R. D. E.) 63–90 (Plenum, New York, 1993).
- 16. Rayner, J. M. V. The cost of being a bat. Nature 350, 383-384 (1991).
- Gould, E. Evidence for echolocation in the Tenrecidae of Madagascar. Proc. Am. Phil. Soc. 109, 352– 360 (1965).
- Tomasi, T. E. Echolocation by the short-tailed shrew Blarina brevicauda. J. Mammal. 60, 751–759 (1979).
- Forsman, K. A. & Malmquist, M. G. Evidence for echolocation in the common shrew, Sorex araneus J. Zool. Lond. 216, 655–662 (1988).
- Speakman, J. R & Racey P. A. No cost of echolocation for bats in flight. *Nature* 350, 421–423 (1991).
 Kalko, E. K. V. Coupling of sound emission and wing-beat in naturally foraging European pipistrelle (*Microchiroptera*: Vespertilionidae). *Folia Zool.* 43, 363–376 (1994).
- Springer, M. S. *et al.* Endemic African mammals shake the phylogenetic tree. *Nature* 388, 61–64 (1997).
- Stanhope, M. J. et al. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proc. Natl Acad. Sci. USA 95, 9967–9972 (1998).
- Kishino, H. & Hasegawa, M. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order within Hominoidea. J. Mol. Evol. 29, 170–179.
- Templeton, A. R. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37, 221–244 (1983).
- Lyons-Weiler, J., Hoelzer, G. A. & Tausch, R. J. Relative Apparent Synapomorphy Analysis (RASA) I: the statistical measurement of phylogenetic signal. *Mol. Biol. Evol.* 13, 749–757 (1996).

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bellar activity was measured by functional magnetic resonance imaging. As predicted by our theory, two types of activity were observed. One was spread over wide areas of the cerebellum and was precisely proportional to the error signal that guides the acquisition of internal models during learning. The other was confined to the area near the posterior superior fissure and remained even after learning, when the error levels had been equalized, thus probably reflecting an acquired internal model of the new tool.

Most neuroimaging studies have found that the regional blood flow in the human cerebellum increases significantly at the beginning of learning for a new motor or cognitive task and decreases as the learning proceeds^{16–19}. These results are often interpreted as meaning that the cerebellum is involved only in the early phase of learning and is not a memory site, that is, it does not store internal models. Here we present a different interpretation (see also ref. 15) based on our computational theory and experimental results.

Previous cerebellar learning theories^{20–22} make no specific predictions about the activity of internal models (see Supplementary Information for details). We have proposed that multiple internal models exist and that they compete to learn new environments and tools²³. During the learning, all of these multiple internal models receive a copy of the error signal and only one or a few learn the new transformation, thereby reducing the error signal and localizing the new activity to a distinct region of the cerebellum. The two types of



Figure 1 Changes in cerebellar activity predicted by the learning theory of internal models. **a**, Signal intensity change caused by error signals (red curve). **b**, Activity maps of the initial and late stages of learning. Each small square represents a unit of multiple internal models. Orange squares indicate regions where the internal model is acquired. **c**, Signal intensity change in the regions where the internal model is acquired. Orange curve indicates activity in the orange squares (the sum of activity reflecting error signals (red curve) and that reflecting the acquired internal model (cyan curve)).

Human cerebellar activity reflecting an acquired internal model of a new tool

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Theories of motor control postulate that the brain uses internal models of the body to control movements accurately. Internal models are neural representations of how, for instance, the arm would respond to a neural command, given its current position and velocity¹⁻⁶. Previous studies have shown that the cerebellar cortex can acquire internal models through motor learning⁷⁻¹¹. Because the human cerebellum is involved in higher cognitive function¹²⁻¹⁵ as well as in motor control, we propose a coherent computational theory in which the phylogenetically newer part of the cerebellum similarly acquires internal models of objects in the external world. While human subjects learned to use a new tool (a computer mouse with a novel rotational transformation), cere-

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cerebellar activity representing the error signals and the internal model are predicted to occur in specific spatio-temporal patterns (Fig. 1). Large error signals are fed into broad regions for all possible internal model candidates at the initial learning stage (red and orange in Fig. 1b). Because the subject's performance improves and the error signals decrease with learning, activity reflecting the error signals also decreases with learning (Fig. 1a). This prediction agrees with previous imaging data. However, signals representing the acquired internal model must increase (cyan curve in Fig. 1c) and remain even at the late stages of learning only in the limited region (orange in Fig. 1b). This region contains a group of the most accurate internal models. Even in this region, total activity is expected to decrease (orange curve in Fig. 1c) because the observed activity is the sum of the error signal (broken red curve) and the internal model (cyan curve). However, significant activity must remain even after the learning is complete. In our interpretation, the activity reflecting the learned model is smeared by the strong activity reflecting the error signal and, therefore, was not detected in previous imaging studies. In our present study, however, we found internal model activity by equalizing the errors under the baseline condition to those under the test condition. Furthermore, the time course of the internal-model activity (cyan curve in Fig. 1c) was estimated by subtracting the error signal activity (red curve) from the total activity (orange curve).

The task for the subjects was to manipulate a computer mouse so that the corresponding cursor followed a randomly moving target on a screen (Fig. 2a; a tracking task). Seven subjects performed the task for eleven sessions (training sessions). We used functional magnetic resonance imaging (fMRI) to scan the cerebellum in the odd-numbered sessions. Each session lasted 9 min and 23 s and comprised eight alternating blocks of test and baseline periods. During the test periods, the cursor appeared in a position rotated 120° around the centre of the screen to necessitate subject learning (novel mouse); during the baseline periods, it was not rotated (ordinary mouse). In the first session (Fig. 2b), large regions near the posterior superior fissure in the lateral cerebellum were significantly more active during the test periods than the baseline periods (correlation coefficient (CC) > 0.3); in the last session (Fig. 2c), only restricted subregions were activated. We confirmed that this activity cannot be attributed to larger hand movements (Fig. 2d) or larger eye movements in the test than in the baseline periods by showing that hand-movement or eye-movement activity is different from the activity shown in Fig. 2b and c (see also Supplementary Information).



Figure 2 Visuomotor learning task and cerebellar activity. **a**, Rule for changing the relationship between mouse and cursor positions. A cross cursor coloured red or green appears on the screen in the test periods or baseline periods, respectively. The open circles indicate the centres of the screen and the hand space. **b**, Cerebellar activity of a typical subject in the first training session. The colour-coded regions were significantly activated in the test periods (CC > 0.3). The broken lines indicate the posterior superior fissure. **c**, Cerebellar activity of the same subject in the last training session. **d**, Regions that were more active during the tracking task (cursor position was not rotated) than during the task of pursuing the moving target with the eyes but without hand/mouse movements. These active regions are apparently different from those in **b** and **c** and are located in the superior anterior and inferior anterior parts of the cerebellum on the right side, ipsilateral to the hand that was performing the task.





approximately the same as slice 2 in Fig. 2. **b**, The activity that remained when the tracking error was equalized. Top, tracking error (mean \pm s.d.) in the error-equalized session. n.s.: not significant (*F*(1, 6) = 4.52). Bottom, activation map.

The subjects' performances were measured by tracking errors (the distance between the cursor and the target; see Methods). The errors in the test periods decreased significantly as the number of sessions increased, whereas the errors in the baseline periods were constant (upper panel in Fig. 3a). A repeated-measures analysis of variance (ANOVA) on the errors indicated a significant effect of the sessions in the test periods (F(10, 60) = 10.60, P < 0.001) but no significant effect in the baseline periods (F(10, 60) = 0.67). Activation maps (P < 0.05, corrected for multiple comparisons) derived from data across all subjects (Fig. 3a) indicated that the activity in the lateral cerebellum became smaller as learning progressed (see Methods).

The learning during the test periods was sufficient for there to be no significant difference in the tracking error between any pairs of the last three sessions according to the *post hoc* test (at P < 0.001level by Tukey's honestly significant difference method). Thus, the cerebellar activation observed in the late stage of learning should include the activity of the acquired internal model. However, we cannot conclude that the activation solely reflects the internal model because the test error was close to, but significantly larger



Figure 4 Cerebellar activity related to error signals and activity related to the acquired internal model. **a**, Activity change (red circles) in the red and orange regions in **b** in comparison to the decrease in tracking error (black circles). Each curve indicates the exponential function fitted to the circles. **b**, Activity in the red and orange regions was significantly (P < 0.05) correlated with the tracking error in the training sessions. Activity in the blue and orange regions was correlated with a step function representing the internal-model activity in the error-equalized session. **c**, Activity change in the blue and orange regions (blue circle filled by orange). The cyan circle indicates the subtraction of the activity in the red region from that in the blue and orange regions. The black circles and solid curve indicate the tracking error increase (as in **a**). The red broken curve is a duplication of the red curve in **a**.

than, the baseline error (for example, F(1, 6) = 28.52, P < 0.005 on the error in the last training session across all subjects). That is, the activation may partly reflect error signals.

To evaluate this possibility, all of the subjects underwent an 'error-equalized' experiment: the target velocity in the baseline periods was increased so that the baseline error was equal to the test error. Here, we used the linear relationship between error and target velocity (see Methods). As result, there was no significant difference between the test and the baseline errors (Fig. 3b, top). However, regions near the posterior superior fissure were significantly more active during the test periods than during the baseline periods (Fig. 3b, bottom). This activity cannot be related to the tracking error. Moreover, the amount of mouse movement (measured by the cursor trajectory length) and the target velocity in the baseline periods were significantly larger than those in the test periods (F(1, 6) = 38.16, P < 0.001, on average 2.38-fold, and F(1, 6) = 156.63, P < 0.001, on average 2.71-fold, respectively). All of the subjects reported that more effort and attention were needed in the baseline periods than in the test periods. Thus, the significant activity increase in the test period cannot be attributed to the mouse/hand movements, the visual target velocity, attention or effort. The most plausible explanation is that the remaining activity in Fig. 3b reflects the acquired internal models, whereas the decrease in activity as learning progresses (Fig. 3a) may largely reflect the error signals.

To strengthen the above conclusion quantitatively, we examined the time courses of gross signal intensity during all sessions averaged over two regions of interest. First, the error-related region (red and orange in Fig. 4b) was defined as voxels whose signal intensity during all the training sessions was significantly and positively correlated with the tracking error (that is, the estimated regression coefficient was significantly larger than zero, t(5276) > 2.33, P < 0.05 corrected). Second, the internal-model-related region (blue and orange in Fig. 4b) was defined as voxels whose signal intensity during the error-equalized session was significantly and positively correlated with the explanatory variable which takes 1 in the test period scans and 0 in the baseline period scans, and thus represents internal-model activity (t(874) > 2.33, P < 0.05 corrected). Orange voxels were correlated with both the tracking error and the internal model activity. The error-related region is widely spread over the lateral cerebellum, whereas the internal model seems to be acquired only in the restricted subregions.

The relative activity in the red and orange regions (per cent of mean signal increase from the baseline periods, all subjects averaged) decreased as the session number increased (red curve in Fig. 4a) and was highly correlated with the tracking error (per cent of increase from the baseline) indicated by the black curve $(r^2 = 0.82 \text{ for all sessions}, F(1, 5) = 22.87, P < 0.005)$. In contrast, the activity in the blue and orange regions did not markedly decrease (orange curve in Fig. 4c), and its correlation with the error was low ($r^2 = 0.25$, F(1, 5) = 1.68). The signal increase in the blue and orange regions was significantly larger than that in the red and orange regions (F(1, 6) = 7.38, P < 0.05). These data indicate that the activity in the blue and orange regions may include components that cannot be explained solely by the error. The cyan curve in Fig. 4c shows the subtraction of the red curve from the orange curve, and represents the internal model activity according to our theory. This activity increased at the initial phase of learning and remained high even in the late learning stage where the error was equalized (Fig. 4c, right).

The acquired internal models in these experiments are expected to represent the altered relationship between the cursor movement and the mouse movement (forward and/or inverse kinematics models of the novel tool). We believe that these internal models were stored in different regions from those for an ordinary mouse, as no significant activity was observed near the posterior superior fissure when the subjects used an ordinary mouse in the test periods

and pursued the moving target with the eyes but without hand/ mouse movements in the baseline periods (see Fig. 2d and Supplementary Information). According to an electrophysiological study in monkeys²⁴, regions near this fissure receive parallel fibre inputs from the premotor and parietal association cortex, and are thus suitable to represent kinematic models of tools. The bilateral activity (see ref. 25 for related bilateral activity) may indicate that activated regions acquire internal models for cognitive function independent of the ipsilateral correspondence between the motor apparatus and the cerebellum. Whereas previous neurophysiological experiments indicated that internal models for the motor apparatus are present in phylogenetically older parts of the cerebellum (such as the ventral paraflocculus, vermis and intermediate parts)⁸⁻¹¹, internal models of objects and tools in the external world seem to reside in newer parts. We further speculate that the cerebellum assists information processing in cerebral areas by providing general internal models of extended controlled objects in the external world such as concepts, symbols and languages. \Box

Methods

Task

The subjects moved a computer mouse (PocketEgg, Elecom) using the right hand while lying in an MRI scanner. Head movements were restrained by a bite bar. They used a tilted mirror to view a rear-projection screen outside the scanner. A colour projector (VPH-12720J LCD; Sony) controlled by a computer (PC-9821 AP2; NEC) displayed the target and the cursor on the screen. During the tracking task, a small white square target was presented on a dark background. The *x* and *y* components of the target path were each subjects moved a small cross-hair cursor on the screen with the mouse. The cursor position was sampled at 60 Hz. The distance between the cursor and the target at each sampling point was accumulated over 4.4 s (tracking error).

Subjects

Ten neurologically normal subjects (20–34 years of age; five females and five males) participated in the experiments. Each participant gave informed written consent. Seven of the subjects (five right-handed and two left-handed²⁶) underwent the training sessions and the error-equalized experiment. The other three subjects (two right-handed and one left-handed) underwent the training sessions and control experiments. In the control experiments, we confirmed that the activity observed in the above seven subjects could not be attributed to differences in hand or eye movements (see Fig. 2d and Supplementary Information).

MRI acquisition

A 1.5-T MRI scanner (Magnetom Vision; Siemens) was used to obtain blood oxygen level-dependent contrast functional images. Images weighted with the apparent transverse relaxation time (T_2^*) were obtained with an echo-planar imaging sequence (repetition time (TR) 4.4 s, echo time (TE) 66 ms, flip angle (FA 90°, field of view (FoV) 240 mm × 240 mm, matrix size 128 × 128). We selected ten axial slices (thickness 7 mm, slice gap 0.21 mm) encompassing the cerebellum. We scanned 128 functional images for each slice during one session. Anatomical images for these slices were obtained with a T_1 weighted sequence (TR 350 ms, TE 6 ms, FA 90°, FoV 240 mm × 240 mm, matrix size 256 × 256).

MRI analysis

Motion artefacts in all functional images were removed by using Automated Image Registration (AIR) version 3.0 (ref. 27). We used two approaches to analyse the functional images: a correlation analysis on a pixel-by-pixel basis²⁸ and an analysis based on the general linear model as implemented in SPM99b (Wellcome Department of Cognitive Neurology). Details of the correlation analysis have been reported in ref. 29. To analyse group data, functional images of each subject's cerebellum were stereotactically transformed to a standard template in SPM, and were smoothed with a gaussian kernel 4 mm full width at half maximum (FWHM). In the activation analyses shown in Fig. 3, condition-specific effects were estimated with the linear model with a boxcar wave form. Areas of significant change in brain activity were specified by linear contrasts of the condition-specific effects and determined using the t-statistics (SPM $\{t\}$). Results were thresholded at t-value 2.33. In assessing the statistical significance of each cluster, we corrected for multiple comparisons based on random gaussian field theory in terms of spatial extent and/or peak height (P < 0.05). Voxel time series were temporally smoothed with a gaussian filter (FWHM of 4 s). We used the effective degree of freedom adjusted for analysis of fMRI time-series³⁰. In the activation analyses shown in Fig. 4b, the explanatory variable of main interest was either the tracking error or the internal model activity.

Equalization of the tracking error according to the relationship between the error and the target velocity

The subjects performed the tracking task under various target velocities for about 15 min. The cursor position was not rotated during this task. The averaged target velocity $(21.30^{\circ} \text{ s}^{-1})$ used in the training sessions was multiplied by a value ranging from 1.0 to 5.0 at intervals of 0.2. Therefore, the target moved at 21 different averaged velocities in random order. Then, the relationship was estimated linearly by the least-squares method. The effect of the velocity on the error was significant ($r^2 > 0.70$, F(1, 19) > 45.27, P < 0.0001) for each subject. When the cerebellar activity was scanned, the target velocity was increased in the baseline period using this relationship, so that the baseline error was equal to the mean error in the preceding test period.

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- Kawato, M., Furukawa, K. & Suzuki, R. A hierarchical neural-network model for control and learning of voluntary movement. *Biol. Cybern.* 57, 169–185 (1987).
- Lackner, J. R. & Dizio, P. Rapid adaptation to Coriolis force perturbations of arm trajectory. J. Neurophysiol. 72, 299–313 (1994).
- Shadmehr, R. & Mussa-Ivaldi, F. A. Adaptive representation of dynamics during learning of a motor task. J. Neurosci. 14, 3208–3224 (1994).
- Wolpert, D. M., Ghahramani, Z. & Jordan, M. I. An internal model for sensorimotor integration. Science 269, 1880–1882 (1995).
- Imamizu, H., Uno, Y. & Kawato, M. Internal representations of the motor apparatus: implications from generalization in visuomotor learning. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 1174–1198 (1995).
- Gomi, H. & Kawato, M. Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement. *Science* 272, 117–120 (1996).
- Kawato, M. & Gomi, H. A computational model of four regions of the cerebellum based on feedbackerror learning. *Biol. Cybern.* 68, 95–103 (1992).
- Shidara, M., Kawano, K., Gomi, H. & Kawato, M. Inverse-dynamics model of eye movement control by Purkinje cells in the cerebellum. *Nature* 365, 50–52 (1993).
- Gomi, H. et al. Temporal firing patterns of Purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys I. Simple spikes. J. Neurophysiol. 80, 818–831 (1998).
- Kobayashi, Y. *et al.* Temporal firing patterns of Purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys II. Complex spikes. *J. Neurophysiol.* 80, 832–848 (1998).
- Kitazawa, S., Kimura, T. & Yin, P. B. Cerebellar complex spikes encode both destinations and errors in arm movements. *Nature* 392, 494–497 (1998).
- Raichle, M. E. et al. Practice-related changes in human brain functional anatomy during nonmotor learning. Cereb. Cortex 4, 8–26 (1994).
- Kim, S. G., Ugurbil, K. & Strick, P. L. Activation of a cerebellar output nucleus during cognitive processing. *Science* 265, 949–951 (1994).
- Allen, G., Buxton, R. B., Wong, E. C. & Courchesne, E. Attentional activation of the cerebellum independent of motor involvement. *Science* 275, 1940–1943 (1997).
- Thach, W. T. On the specific role of the cerebellum in motor learning and cognition: Clues from PET activation and lesion studies in man. *Behav. Brain Sci.* 19, 411–431 (1996).
- Friston, K. J., Frith, C. D., Passingham, R. E., Liddle, P. F. & Frackowiak, R. S. Motor practice and neurophysiological adaptation in the cerebellum: a positron tomography study. *Proc. R. Soc. Lond. B Biol. Sci.* 248, 223–228 (1992).
- Grafton, S. T., Woods, R. P. & Tyszka, M. Functional imaging of procedural motor learning: relating cerebral blood flow with individual subject performance. *Hum. Brain Mapp.* 1, 221–234 (1994).
 Seitz, R. J. *et al.* Successive roles of the cerebellum and premotor cortices in trajectorial learning.
- NeuroReport 5, 2541–2544 (1994).
- Flament, D., Ellermann, J. M., Kim, S. G., Ugurbil, K. & Ebner, T. J. Functional magnetic resonance imaging of cerebellar activation during the learning of a visuomotor dissociation task. *Hum. Brain Mapp.* 4, 210–226 (1996).
- 20. Marr, D. A theory of cerebellar cortex. J. Physiol. (Lond.) 202, 437-470 (1969).
- 21. Albus, J. S. A theory of cerebellar function. Math. Biosci. 10, 25-61 (1971).
- Ito, M. Cerebellar control of the vestibulo-ocular reflex—around the flocculus hypothesis. Annu. Rev. Neurosci. 5, 275–296 (1982).
- Wolpert, D. M. & Kawato, M. Multiple paired forward and inverse models for motor control. *Neural Netw.* 11, 1317–1329 (1998).
- Sasaki, K. *et al.* Mossy fibre and climbing fibre responses produced in the cerebellar cortex by stimulation of the cerebral cortex in monkeys. *Exp. Brain Res.* 29, 419–428 (1977).
- Roland, P. E., Eriksson, L., Widen, L. & Stone-Elander, S. Changes in regional cerebral oxidative metabolism induced by tactile learning and recognition in man. *Eur. J. Neurosci.* 1, 3–18 (1988).
- Oldfield, R. C. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113 (1971).
- Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R. & Mazziotta, J. C. Automated image registration: I. General methods and intrasubject, intramodality validation. *J. Comput. Assist. Tomogr.* 22, 139–152 (1998).
- Bandettini, P. A., Jesmanowicz, A., Wong, E. C. & Hyde, J. S. Processing strategies for time-course data sets in functional MRI of the human brain. *Magn. Reson. Med.* 30, 161–173 (1993).
- Tamada, T., Miyauchi, S., Imamizu, H., Yoshioka, T. & Kawato, M. Cerebro-cerebellar functional connectivity revealed by the laterality index in tool-use learning. *NeuroReport* 10, 325–331 (1999).
- Worsley, K. J. & Friston, K. J. Analysis of fMRI time-series revisited—again. *Neuroimage* 2, 173–181 (1995).

Supplementary information is available on *Nature's* World-Wide Web site (http:// www.nature.com) or as paper copy from the London editorial offices of *Nature*.

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news and views



Figure 2 Fish braincases in lateral view, showing the eyestalk, or its base or site of attachment (all marked as E; see also Fig. 2 on page 186). The eyestalk is a diagnostic feature that was thought to be unique to chondrichthyans and placoderms, but is evident in Basden and colleagues' fish¹. a, *Chlamydoselachus* (chondrichthyan), a recent shark⁵. b, *Jagorina*, a placoderm⁶. c, *Brindabellaspis*, a placoderm¹. O, the opening for the optic nerve.

matching the condition in *Jagorina*. So there is no doubt that AMF101607 had an eyestalk. In consequence, eyestalks can no longer be considered to be unique to chondrichthyans and placoderms.

This is not a trivial point. Changing knowledge about the distribution of key characteristics often radically alters our understanding of the evolutionary relationships of their bearers. Take feathers, for example — as soon as it was found that theropod dinosaurs possessed them, feathers could no longer be regarded as unique to birds. The revelation that the new fish from Australia had an eyestalk has similar significance (if less public appeal).

Based on the cranial features of AMF-101607 and of examples of other groups in the evolutionary tree constructed by Zhu *et al.*², and using a computer program called PAUP, Basden *et al.* produced several alternative positions of their fish and *Psarolepis* in the tree (see Fig. 3 on page 187). Their preference is for one with the new form at the base of the bony fishes and *Psarolepis* at the base of the lobe-finned fishes.

Uncertainty about the positions of the two forms in Basden and colleagues' tree arises mainly from insufficient information. Specimen AMF101607 is very similar to the two Late Devonian ray-finned fishes, so we ought to compare them more thoroughly. The eyestalk-attachment area in AMF-101607 seems to occupy exactly the same position as the opening for the optic nerve in *Mimia* and *Moythomasia* (and is almost

the same shape and size), so it could be that these fishes also had an eyestalk. Comparison of the new form with *Mimia* and *Moythomasia* will help to identify the closest relative of bony fishes, and may even tell us something about the evolution of jawed vertebrates as a whole.

Other new knowledge also has to be taken into account. The characters previously held to be unique to osteichthyans have recently been identified in a chondrichthyan from Bolivia⁸, and a molecular study places the cartilaginous fishes within the bony-fish evolutionary tree⁹. All of these developments challenge our understanding of the relationships among the major groups of primitive back-boned animals and demand a profound change of conventional wisdom. The new form reported by Basden *et al.* is a welcome addition to the list of candidates for the position of 'ancestor' of the bony fishes. But whether it will be elected remains to be seen.

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- Basden, A. M., Young, G. C., Coates, M. I. & Ritchie, A. Nature 403, 185–188 (2000).
- Zhu, M., Yu, X. & Janvier, P. Nature 397, 607–610 (1999).
- 3. Yu, X. J. Vert. Paleontol. 18, 261-274 (1998).
- Gardiner, B. G. Bull. Brit. Mus. Nat. Hist. (Geol.) 37, 173–428 (1984).
- 5. Allis, E. P. Acta Zool. 4, 123-221 (1923).
- Stensiö, E. in *Traité de Paléontologie* IV, Vol. 2 (ed. Piveteau, J.) 71–692 (Masson, Paris, 1969).
- 7. Young, G. Palaeontolgraphica 167A, 10-76 (1980).
- 8. Janvier, P. Trends Ecol. Evol. 14, 298-299 (1999).
- Rasmussen, A.-S. & Arnason, U. J. Mol. Evol. 48, 118–123 (1999).

Internal model visualized

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ow can we instantly recognize a familiar object? Probably because, in the brain, we already have a model of that object which is activated through vision. Similarly, we can quickly comprehend what we hear because the brain is likely to contain a model representing the meanings of the sounds we encounter. And we can probably carry out complex movements so easily and accurately because the cerebellum provides a model of what is to be moved. Such internal models provide an attractive explanation for the brain's subtle cognitive and control mechanisms, but there has been no way to investigate them experimentally. Now, however, on page 192 of this issue, Imamizu et al.¹ report a set of brain-imaging data that

provide the first evidence for such a model being formed in the cerebellum.

The basis of the work done by Imamizu *et al.* is the unique theory² of the adaptivecontrol system with two degrees of freedom (Fig. 1). It works like this. When we move a hand, a desirable movement worked out somewhere in the brain is conveyed as an instruction to the motor area and its related regions in the cerebral cortex. These areas in turn generate command signals, which act on the hand/arm system to carry out the movement. Information about the realized movement is conveyed through the visual system back to the motor and related areas, and compared with the movement received as an instruction. This feedback ensures that



Figure 1 Block diagram of the two degrees of freedom adaptive-control system with feedback-error learning mechanism. This system combines a feedback control by the cerebral cortex and a feedforward control by the cerebellum. The cerebral cortex compares the instructed, desired movement with a realized movement by sensory feedback, whereas the cerebellum receives only the instruction. To realize a desired movement without feedback of the realized movement, the cerebellum needs to form an inverse model of the hand/arm system, as visualized by Imamizu *et al.*¹ using brain-imaging data. (Modified from ref. 2.)

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Figure 2 Basic structure of the neuronal circuitry in the cerebellum. A single functional 'unit' is shown. Mossy-fibre signals provide inputs to the unit and neurons in the cerebellar nucleus generate outputs. Climbing-fibre signals represent errors, reorganizing internal connections within the unit to modify its input–output relationship. LTD, long-term depression. (Adapted from ref. 3.)

the realized movement is similar to the 'instruction' movement. The instruction may also be converted to command signals by the cerebellum, instead of by the cerebral cortex.

Even without such feedback, this pathway could produce a movement that closely matches the movement received as an instruction. For this to happen, however, the cerebellum would need to contain the inverse of the dynamics or kinematics of the hand/arm system — in other words, the cerebellum would need to contain an inverse model of the hand/arm system. The model is formed and updated through learning, by referring to the errors between the intended and performed movements, as detected by the motor and related areas of the cerebral cortex (feedback-error learning)².

To test this hypothetical prediction, Imamizu et al.¹ asked a human subject lying in a functional magnetic resonance imaging (fMRI) scanner to manipulate a computer mouse. During the so-called 'baseline' period, the subject followed a moving square target with a cross-hair cursor on a screen. Then, during the test, the position of the cursor was rotated 120° around the centre of the screen to provide a new mouse 'condition'. At first, during the test period, large regions of the cerebellum were significantly activated compared with their activity during the baseline period. But this activation decreased after repeated test trials, in parallel with a reduction of the tracking errors. However, certain restricted sub-regions of the brain (near the posterior superior fissure) continued to be activated. The authors propose that this remaining activity represents an internal model that is formed during the repeated test trials. This model defines the

new relationship between movement of the cursor and of the mouse.

The internal-model concept for motor learning is reasonable if we consider the known cellular mechanisms of the cerebellum. The cerebellum has a compartmentalized structure that consists of numerous small, functional units, each of which contains a neuronal network, composed of Purkinje and other neurons, organized in a geometrically beautiful way (Fig. 2). Each unit can change its input-output relationship through learning, which is driven by error signals conveyed to the Purkinje cells by a unique input structure, the climbing fibres. Climbing-fibre signals induce longterm depression (LTD) of transmission from a major input to the Purkinje cells, via the mossy fibre-parallel fibre pathway³. LTD depresses those synapses between the parallel fibres and Purkinje cells that are involved in making errors, thereby reorganizing internal connections towards a reduction of the errors. Through this learning mechanism a cerebellar unit could modify its inputoutput relationship until it represents the model required for precise control.

A crucial question is whether an increase in local blood flow in the cerebellum, as detected by fMRI, really represents the formation and maintenance of an internal model. If LTD is the only synaptic plasticity that underlies the learning mechanism of the cerebellar circuitry, the learning is unlikely to be accompanied by an increase in electric impulse discharges (which may be reflected as increased local blood flow). So the authors assume that excitatory and inhibitory synaptic transmissions to the Purkinje cells are facilitated, and that electric-impulse discharges of the Purkinje cells increase.

But in the complex neuronal circuitry of the brain there may be other possibilities. For example, many chemical reactions underlie the induction of LTD, including the release of nitric oxide, which has a well-known action of relaxing blood capillaries. The next question to address experimentally is how not only the electric-impulse discharges, but also the complex chemical processes, contribute to increases in local blood flow in the cerebellum.

As neuroscientists strive to understand the molecular and cellular events that occur in neurons, effective technologies and methodologies for experimentally investigating computational and cognitive principles of the brain are still in short supply. The success of Imamizu *et al.*¹ in visualizing an internal model in the cerebellum should therefore provide tremendous encouragement for other researchers in the field. ■ *Masao Ito is at the Brain Science Institute, RIKEN, Wako, Saitama 351-0198, Japan. e-mail: masao@mailsv.brain.riken.go.jp*

- 2. Kawato, M. & Gomi, H. Biol. Cybern. 68, 95-103 (1992).
- 3. Ito, M. Trends Cog. Sci. 2, 313-321 (1998).

Coal, air, fire and water

Coal-mining is a costly, labour-intensive activity. Many attempts have been made to extract at least some of the energy of coal *in situ*, by underground gasification. Daedalus is now updating this idea.

A coal mine, he points out, fills with water unless constantly pumped out. In a flooded mine the water is under hydrostatic pressure. At the bottom of a mine more than about 2.2 km deep, it would reach supercritical pressure. Heated, it could not boil, but would go to supercritical water — a powerful solvent and reaction medium. If it contained dissolved oxygen, organic materials including coal would burn spontaneously in it. So, says Daedalus, drill two holes down to a sufficiently deep coal seam, lower some sort of robot borer to drill a tunnel connecting the two holes, and fill the whole thing with water. Ignite the coal electrically or pyrotechnically, and pump aerated water down one shaft and up the other. The water flow will then deliver the products to the surface.

What will those products be? In the presence of excess fuel - such as a vast coal seam — supercritical combustion is a very partial business. Toluene, for example, burns in limited oxygen to benzoic acid. Coal will go to big aromatic or quinonoid molecules, with enough oxygen in them to dissolve in the water. The upcoming stream of hot water will boil as the hydrostatic pressure lessens. The steam will contain the more volatile organics, easily separable by fractionation, ideally by stepwise expansion in a steam engine. Bigger molecules will stay in the water: some will crystallize out as it cools. So the mine will yield steam power, plus a stream of useful fuels and chemical feedstocks. Sulphur dioxide in the water will be processed to useful sulphuric acid, and solid ash will mainly stay underground.

A supercritical mine will access a vast amount of coal. The initial narrow tunnel will soon widen laterally as it eats the seam away from between the rocky strata above and below it. As it widens, the tunnel will slowly collapse in the middle by subsidence, giving two tunnels. These will gradually move apart through the seam, scouring it out as subsidence propels them sideways. The vast coal reserves more than 2.2 km down, too deep for normal mining, will be accessible at last. David Jones

The Further Inventions of Daedalus (Oxford University Press), 148 past Daedalus columns expanded and illustrated, is now on sale. Special *Nature* offer: m.curtis@nature.com

^{1.} Imamizu, H. et al. Nature 403, 192–195 (2000).